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An Introduction to the Pteridophyte Flora of Finca La Selva, Costa Rica

MICHAEL H. GRAYUM
Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166
HUGH W. CHURCHILL
Department of Botany, University of Vermont, Burlington, Vermont 05405

Finca La Selva, now more properly known as the La Selva Biological Station, is the flagship field station of the Organization for Tropical Studies (OTS) in Costa Rica. A comprehensive floristic inventory of La Selva was initiated in 1979 (Hammel & Grayum, 1982), and a technical flora has recently begun to appear in fascicle form in the journal *Selbyana* (see Wilbur, 1986). The recent completion of the pteridophyte treatments for this flora (Grayum & Churchill, 1988a, 1988b; here summarized in Appendix 1) permits the present informal introduction and analysis.

THE SITE

Finca La Selva is located in the Caribbean lowlands of Costa Rica, in the zone where the volcanic Central Cordillera begins to rise up out of the swampy coastal plain. The Station occupies 1533 hectares at the confluence of the Ríos Puerto Viejo and Sarapiquí. The elevation on the property ranges from about 35 m (where the rivers meet) to 130 m on the higher ridges toward the South Boundary. Recent alluvial soils occur along the rivers and lower portions of the major quebradas (creeks), but volcanically derived soils predominate elsewhere. The major habitat at La Selva is upland primary forest; however, several other habitats are represented, including swamp forest, open marshes, streamsides and riparian forest, alluvial forest, secondary forest, and weedy areas (see Appendix 1).

La Selva lies in one of the wettest parts of Costa Rica, receiving an average of about 3900 mm of rain per year. Although there is a slight dry season from January through April, it is not nearly so pronounced as that experienced on Costa Rica's Pacific slope during these months.

More detailed descriptions and additional information can be found in numerous other sources (e.g., Grayum, 1982; Hartshorn, 1983; Hammel, 1986; Wilbur, 1986).

HISTORY OF PTERIDOPHYTE COLLECTING AT LA SELVA

The earliest known pteridophyte collections from on or very near the site now known as La Selva were made during the "Golden Period" of Costa Rican natural history (see Gómez & Savage, 1983), around the turn of the century. Pablo Biolley and Henri Pittier, Swiss botanists based in San José, visited the "confluence of the Río Puerto Viejo and Sarapiquí" at least twice, in April, 1892 and February,

1893, making general plant collections. Among the ferns collected by Biolley and Pittier were two species, *Pteris quadriaurita* and *Pityrogramma tartarea*, that have not since been recollected from La Selva.

During most of the first half of the present century, natural history languished in Costa Rica for a variety of reasons (Gómez & Savage, 1983), and little or no botanical fieldwork was undertaken in the La Selva vicinity. The next pteridophyte collections on record from La Selva are those of Edith Scamman, a fern specialist associated with Harvard's Gray Herbarium, who visited Costa Rica in 1951, 1953, 1955, and 1956, amassing a total of about 1400 specimens (Tryon & Tryon, 1968). Herbarium labels indicate that Scamman collected ferns at La Selva (then the property of Dr. Leslie R. Holdridge) on at least one occasion, from 18–28 February 1955; however, the exact number of specimens collected at the site is difficult to establish from this source.

By 1967 Finca La Selva had become OTS property, and in the summer of that year OTS conducted a field course on the biology of tropical pteridophytes in Costa Rica (Mickel, 1967). This course was coordinated by Dr. John T. Mickel, and included Drs. Elías de la Sota, Warren H. Wagner, Jr., A. Murray Evans and David B. Lellinger as full- or part-time faculty. The list of participants in the course, including "ten outstanding students . . . selected from nine universities across the United States," now reads like a "Who's Who in American Pteridology." During a few days at La Selva in mid-August, this group produced the first checklist of La Selva pteridophytes (OTS, 1967), accounting for 89 of the 173 species presently known. De la Sota (1971) later published a list of the 56 epiphytic species then known from La Selva.

During the interval from 1967 to 1979, minor pteridophyte collections were made at La Selva by individuals too numerous to mention, including many of those involved in the 1967 course. The Costa Rican pteridologist Luis Diego Gómez visited the site on many occasions, making several significant collections and compiling a checklist, circulated by OTS during the mid- and late 70s, that enumerated 100 pteridophyte species. From March to September of 1978, the first author made numerous collections of pteridophytes and other groups at La Selva.

The "Flora of La Selva" project was officially inaugurated in 1979, and in the summer of that year the first author worked as the first collector for that project. Intensive general collecting was pursued at La Selva from that time until about 1985, and collecting continues, albeit spottily, to the present. A number of collectors have been involved in this effort, chief among them Barry Hammel, Robert L. Wilbur, James Folsom, Tim McDowell, Brian Jacobs, Isidro Chacón, Damon Smith, and John Sperry. The first set of this material is deposited at DUKE.

In March, 1985, June Barcock prepared approximately 100 fern specimens during the visit of "Operation Raleigh" to La Selva. This collection, deposited at Kew, is significant in that it was made in a poorly explored area of the property; moreover, some specimens were obtained from the canopy by means of a platform constructed by the group. In addition to several rare species, two species new to the flora (*Trichomanes crispum* and *Blechnum polypodioides*) were collected.

TABLE 1. Total Number of Pteridophyte Species in Selected Floras.

Place	Area (km²)	Pterid. spp.	Authority
California	411,013	86	Grillos, 1966
Texas	692,405	107	Correll, 1956
Chihuahua	245,612	126	Knobloch & Correll, 1962
Florida	151,670	135	Lakela & Long, 1976
Zambia	752,614	146	Kornaś, 1979
La Selva	**15**	**173**	**Grayum & Churchill, 1988a, b**
Hong Kong	1,034	175	Edie, 1978
Puerto Rico	8,897	263	Kepler, 1975
Australia	7,686,849	416	Jones & Clemesha, 1981
Jamaica	10,962	579	Proctor, 1985
Chiapas	ca. 74,000	609	Smith, 1981
Costa Rica	50,900	ca. 900	Grayum, unpubl. data

THE PTERIDOPHYTE FLORA: GENERAL REMARKS

At the present time, 173 species of pteridophytes in 45 genera are known from Finca La Selva, ranking this tiny site respectably high among several much larger political units (see Table 1) selected more or less randomly on the basis of ease of extraction of comparable data. Seven additional species, including one additional genus (*Dicranopteris*), have been collected immediately adjacent to La Selva and have been considered likely hypotheticals and treated in full for the Flora. Two further species, *Antrophyum lineatum* and *Grammitis turrialbae*, are vouchered for La Selva by a single correctly identified specimen each; however, both are mid- to high-elevation species and label mixups are strongly suspected.

Particularly surprising is the comparison of the La Selva pteridoflora with that of Florida (Table 1), the most tropical of the continental 49 states and about 10,000 times the size of La Selva, but with 21.5% fewer pteridophyte species.

In view of the thoroughness with which La Selva has been botanically inventoried, the above figures probably represent a reasonably close approximation of the actual totals. Clearly, however, they are not exact, nor can we ever hope to make them so. Although the area of La Selva is quite small, the terrain is rugged and complex. Large areas of the reserve are inaccessible by trail, and most of these have been only cursorily explored. Certain parts of the so-called "Western Annex," added to La Selva in 1982, remain completely unexplored.

More intensive collecting along creeks and on ridges in the more remote and relatively poorly explored southern portions of La Selva will certainly yield new fern records (as demonstrated by the Barcock effort discussed previously). This seems especially likely when one considers the highly localized distribution patterns characteristic of many plant species in the La Selva rain forest, contrary to what one might predict of this superficially uniform environment. For example, 33 (about 19%) of the 173 pteridophyte species presently known from La Selva are classed as "very rare" (known from just one or two collections; see Appendix 1), including such conspicuous ferns as *Metaxya rostrata* and *Thelypteris gigan-*

tea; an additional 45 species (26% of the total) are considered rare (known from 3–5 collections). Thus about 45% of the La Selva fern flora consists of species unlikely to be encountered by the short-term visitor (interestingly, roughly the same fraction unaccounted for by the 1967 course). These figures are surprising in view of the "notorious" ease with which fern spores are dispersed in the air (Smith, 1972; Gentry & Dodson, 1987); however, comparable numbers for the likewise air-dispersed Orchidaceae at La Selva may be higher yet (J. Atwood, pers. comm.). Hammel (1986) reported that about 75% of the La Selva species in six angiosperm families with more conventional seed-dispersal modes "are known from a few individuals or from a few small populations."

The inherently dynamic nature of natural floras presents an additional obstacle to a precise inventory of the La Selva pteridophytes. Certain habitats seem especially subject to ostensibly temporary colonization by basically extralimital species, pteridophytes and spermatophytes alike. Such habitats include recently disturbed or weedy sites in primary or secondary forest and, especially, the banks of the Ríos Puerto Viejo and Sarapiquí, regularly disturbed by landslides and diaspore-bearing floodwaters. The distribution at La Selva of species such as *Blechnum fraxineum*, *Dennstaedtia cicutaria*, and *Thelypteris resinifera* suggests ephemeral occurrence in the latter habitat. This may also be the case with *Pityrogramma tartarea* and *Pteris quadriaurita*, not recollected in the La Selva vicinity for nearly a century.

The air-dispersed diaspores of pteridophytes perhaps render the La Selva pteridophyte flora more dynamic than the spermatophyte flora. This is suggested by recent discoveries of species new to the flora in heavily collected sites, e.g., *Stigmatopteris longicaudata* along the Quebrada El Taconazo and, most dramatically, *Ophioglossum reticulatum* in the laboratory clearing.

A particularly striking feature of the La Selva fern flora that is also probably attributable to the high vagility of air-dispersed plants is the dearth of undescribed species. In fact, just one La Selva pteridophyte species (an *Elaphoglossum*) is believed to be new to science (although a few others, such as *Diplazium pactile* and *D. striatastrum*, were described within the last decade). Similarly, only a single La Selva orchid species (out of 113) is apparently undescribed (J. Atwood, pers. comm.). This is markedly in contrast with the situation for spermatophytes in general: for example, 12 (about 10%) of the 123 species in the subset of six angiosperm families analyzed by Hammel (1986) were described by Hammel himself, and over 50 new species of seed plants have been described from La Selva altogether (Wilbur, 1986).

The La Selva pteridoflora also includes but two apparent country records (*Danaea grandifolia* and *Bolbitis aliena*), contrasting with the spermatophyte flora (Grayum & Hammel, 1982) in this respect as well.

Before proceeding with the analysis of the La Selva pteridoflora, an important taxonomic qualification is necessary. The number of pteridophyte genera attributed to La Selva and (to a lesser extent) the number of species depends on one's taxonomic viewpoint. Pteridophytes are notoriously intractable as regards familial and generic classification. For the purposes of the La Selva flora, rather broad circumscriptions were opted for in most cases. Without narrowing these very

TABLE 2. Most Diverse Pteridophyte Genera at Three Neotropical Sites.

LS[1]		BCI		RP	
Genus	Spp.	Genus	Spp.	Genus	Spp.
Thelypteris	18	*Polypodium*	13	*Thelypteris*	11
Polypodium	17	*Trichomanes*	9	*Polypodium*	7
Trichomanes	14	*Adiantum*	9	*Adiantum*	6
Asplenium	11	*Thelypteris*	8	*Asplenium*	5
Selaginella	9	*Selaginella*	6	*Diplazium*	5
Tectaria	9	*Asplenium*	6	*Tectaria*	4
Diplazium	8	*Pteris*	4	*Selaginella*	3
Adiantum	7	*Elaphoglossum*	3	*Trichomanes*	3
Elaphoglossum	6			*Elaphoglossum*	3
				Stigmatopteris	3

[1] Acronyms and data sources: LS = La Selva (Grayum & Churchill, 1988a, b); BCI = Barro Colorado Island (Croat, 1978); RP = Río Palenque (Dodson & Gentry, 1978).

radically, well over a dozen pteridophyte genera (e.g., *Lycopodiella, Huperzia, Trichipteris, Megalastrum, Peltapteris, Cochlidium, Olfersia, Campyloneurum, Phlebodium, Microgramma, Niphidium, Pecluma, Pleopeltis, Christella, Goniopteris, Macrothelypteris, Meniscium, Ananthacorus*) could be added to the La Selva total of 45. An additional species could be appended, raising the total to 174, were *Asplenium auritum* recognized as distinct from *A. cuspidatum* (both entities occur at La Selva).

COMPOSITION OF THE FLORA

Of the 173 La Selva pteridophyte species, 160 (in 43 genera) belong to the Divison Polypodiophyta and 127 (in 35 genera) to the broadly-circumscribed Polypodiaceae, including three weedy species introduced from the Old World (*Nephrolepis multiflora, Thelypteris dentata*, and *T. torresiana*). Polypodiaceae thus reigns as the largest family in the La Selva vascular flora, surpassing the largest angiosperm family, Orchidaceae, which comprises 113 species (and two fewer genera; Atwood, 1986). Furthermore, ferns are conspicuously more abundant than orchids (from an understory perspective, at any rate). Pteridophyte species account for about 9% of the La Selva vascular flora (based on an estimated total of 1900 species; see Wilbur, 1986), which falls in the range of 5–10% given by Smith (1981) for wet tropical forests.

The most diverse pteridophyte genera (hypotheticals excluded) at La Selva are *Thelypteris, Polypodium*, and *Trichomanes*, which would rank among the ten largest genera of La Selva vascular plants based on data presented by Hammel & Grayum (1982). Table 2 lists the largest genera of pteridophytes at La Selva and at two other neotropical sites for which data are available. Pertinent information regarding all three sites is presented in Table 3; additional data may be found in Croat (1978), Dodson and Gentry (1978), and Hammel (1986). All three sites are in the lowlands, at roughly the same elevation. Barro Colorado Island

TABLE 3. Relevant Abiotic Characteristics and Total Number of Pteridophyte Species for Three Neotropical Sites.

Site	Size (ha)	Elev. (m)	Precip. (mm/yr)	Temp. (°C)	No. spp.
RP[1]	167	150–220	2980[2]	20–28	83[3]
BCI	1560	25–165	2750	21–32	104
LS	1533	37–130	3900	24[4]	173

[1] RP = Río Palenque; BCI = Barro Colorado Island; LS = La Selva.
[2] Datum from Dodson, et al. (1985).
[3] Incorporating updates from A. Gentry (pers. comm.).
[4] Mean annual temperature.

(BCI) in Panama is about the same size as La Selva; however, the Río Palenque reserve in Ecuador is an order of magnitude smaller. Both of the last-named two sites are drier and more seasonal than La Selva, BCI markedly so.

Atwood (1986) judged that "La Selva is most similar generically to Río Palenque" in its orchid flora (as compared with BCI and Volcán Mombacho, Nicaragua); Hammel (1986), on the other hand, found La Selva to "share more genera and species" of six angiosperm families with BCI than with Río Palenque. As regards pteridophytes, La Selva shares the same number of genera (34) with BCI and Río Palenque. Five additional genera (*Botrychium, Anemia, Lygodium, Maxonia,* and *Ceratopteris*) occur at Río Palenque, whereas BCI boasts nine genera not known from La Selva (*Lygodium, Schizaea, Cnemidaria, Acrostichum, Ceratopteris, Maxonia, Triplophyllum, Dictyoxiphium,* and *Salvinia*).

Twenty-eight pteridophyte species are shared among all three of the sites (see Appendix 1). Sixty-five of the 104 pteridophyte species at BCI (about 62.5%) are shared with La Selva, while Río Palenque shares 48 species (57.8% of the total 83). Thirty-seven of the species shared by La Selva and BCI do not occur at Río Palenque. More surprising, perhaps, is the fact that 20 species are shared by La Selva and Río Palenque but do not occur at the geographically intermediate BCI station. Moreover, just four species (*Ceratopteris pteridoides, Asplenium laetum, Maxonia apiifolia,* and *Saccoloma elegans*) are common to BCI and Río Palenque but absent from La Selva.

Similarly ambiguous results are obtained when Sorensen's coefficient of similarity (Sarmiento, 1975) is calculated (at the species level) for these three sites. Comparison of the La Selva and BCI pteridofloras yields the highest figure, 47; the coefficient for La Selva/Río Palenque is 38. However, when Río Palenque is compared with BCI, the value is lower still (32).

We believe that the La Selva pteridoflora is probably more similar to that of Río Palenque, but that this relationship is somewhat obscured by the much smaller size of the latter site and the consequent absence of many species that may occur (or have occurred) in the near vicinity. The latter factor casts a long shadow over absolute-number comparisons among the three sites. La Selva and BCI are comparable in size and elevation, and the fact that La Selva has 65% more pteridophyte species than BCI must be explainable in terms of the significant differ-

ences in amount and distribution of precipitation. Gentry (e.g., 1982) has repeatedly emphasized the importance of precipitation in explaining phytogeographical patterns, and noted that the Río Palenque flora is more like that of Central American wet forests than that of nearby but more seasonal forests in western Ecuador. Lellinger (1975) had previously arrived at essentially the same conclusion regarding the Chocó pteridophyte flora.

Although the total annual precipitation at Río Palenque is not much higher than that at BCI, the effects of the dry season at the former site are somewhat mitigated by prevailing cool and cloudy conditions (A. H. Gentry, pers. comm.). Thus, whereas many seed plant taxa become more predominantly epiphytic in wet forest as opposed to moist forest, these preliminary data suggest that pteridophytes apparently do not. The dramatic increase in epiphytic pteridophytes with increasing elevation, discussed in a later section, is perhaps due to some factor other than absolute precipitation; indeed, the average annual rainfall at the cloud-forest reserve at Monte Verde, Costa Rica, is actually considerably lower than at La Selva (G. S. Hartshorn, pers. comm.).

Growth Habit

The only aspect of growth habit that we investigated was the distribution of epiphytic vs. terrestrial (or epipetric) species. We might have predicted, for example, that the higher diversity of such groups as pteridophytes and Araceae (Grayum, 1982) at La Selva, as compared with BCI, was due to conditions at the former site being more conducive to epiphytes in general on account of the higher precipitation (de la Sota, 1971; Gentry & Dodson, 1987). In fact, epiphytes account for nearly twice as large a percentage of the total vascular flora at La Selva than at BCI (Gentry & Dodson, 1987). Surprisingly, however, the percentage of epiphytic species in the La Selva pteridoflora (41.9%) is not significantly different from that at BCI (40.4%), nor in all probability from that at Río Palenque (35.9%). Thus, whereas many seed plant taxa become more predominantly epiphytic in wet forest as opposed to moist forest, these preliminary data suggest that pteridophytes apparently do not. The dramatic increase in epiphytic pteridophytes with increasing elevation, discussed in a later section, is perhaps due to some factor other than absolute precipitation; indeed, the average annual rainfall at the cloud-forest reserve at Monte Verde, Costa Rica, is actually considerably lower than at La Selva (G. S. Hartshorn, pers. comm.).

Distribution of La Selva Pteridophytes by Habitat

Over half of the 123 spermatophyte species in Hammel's (1986) study occurred in upland primary forest. This is also the favored pteridophyte habitat at La Selva, the corresponding figure being 50.0% (86 species). The most common and characteristic species for each La Selva habitat are listed below, along with the percentage of the total pteridoflora represented there (these figures are not additive, since many fern species occur in two or more habitats).

Upland Primary Forest.—*Danaea wendlandii, Trichomanes collariatum, T. godmanii, Cyathea multiflora, Adiantum obliquum, Asplenium cirrhatum, A. cuspidatum, Elaphoglossum palmense, E. peltatum, Grammitis linearifolia, G. serrulata, Hypolepis hostilis, Lomariopsis fendleri, Polybotrya caudata, P. cervina, Polypodium triseriale, Pteris pungens, Saccoloma inaequale, Salpichlaena volubilis, Thelypteris curta, T. lingulata* (50.0%).

Alluvial Forest.—*Selaginella eurynota, S. flagellata, Adiantum tetraphyllum,*

Dennstaedtia bipinnata, Polypodium percussum, Tectaria nicotianifolia, T. rivalis (26.8%).

Riparian Habitats.—*Selaginella atirrensis, S. umbrosa, Cyathea trichiata, Blechnum occidentale, Tectaria mexicana, Thelypteris angustifolia, T. balbisii, T. francoana, T. torresiana* (21.2%).

Secondary Growth.—*Selaginella arthritica, Alsophila cuspidata, A. firma, Antrophyum lanceolatum, Bolbitis portoricensis, Cyclopeltis semicordata, Dicranoglossum panamense, Diplazium striatastrum, Nephrolepis biserrata, Polypodium aureum, P. ciliatum, P. phyllitidis, P. lycopodioides, Tectaria incisa, Thelypteris nicaraguensis* (19.4%).

Swamp Forest.—*Cyathea ursina, Adiantum tetraphyllum, Diplazium lindbergii, D. macrophyllum, Polypodium occultum, P. sphenodes, Tectaria athyrioides* (13.4%).

Rocky Quebradas.—*Selaginella umbrosa, Trichomanes diaphanum, T. krausii, Asplenium otites, A. repandulum, Bolbitis nicotianifolia, Tectaria plantaginea* (12.3%).

Weedy Areas.—*Adiantum latifolium, A. petiolatum, Hemionitis palmata, Hypolepis repens, Pityrogramma calomelanos, Thelypteris dentata, T. nicaraguensis* (6.7%).

Open Marshes.—*Nephrolepis biserrata, Thelypteris serrata* (1.2%).

Additional data can be found in Appendix 1.

Distribution of La Selva Pteridophytes in Costa Rica

Dogma has it that the pteridoflora of lowland tropical sites is boring and not very diverse, comprising mainly common and widespread lowland species (Wagner & Gómez, 1983). This is not strictly the case at La Selva, which is relatively wet and cool due to its location at the foot of the Central Cordillera. This proximity to the mountains makes La Selva an atypical lowland site when compared to many other parts of the lowland tropics.

Based on data culled from the MO and CR herbaria and summarized by Grayum and Churchill (1988a, b), only 30.1% of the species in the La Selva pteridoflora are restricted (in Costa Rica) to the lowlands (i.e., elevations of less than 1000 m); 10.6% are restricted to elevations of less than 500 m; 55.2% range into mid-elevations (1000–2000 m); and 14.5% to higher elevations (above 2000 m). Six species (*Lycopodium cernuum, Selaginella flagellata, Asplenium cuspidatum, A. serra, Blechnum occidentale,* and *Elaphoglossum peltatum*) ascend to 3000 m or higher.

Only 17.9% of La Selva pteridophyte species are confined, in Costa Rica, to the Caribbean slope (not surprisingly, this total includes nearly 75% of the species restricted to below 500 m).

Since we know of no comprehensive enumeration of pteridophyte species for any mid-elevation (e.g., cloud forest) site in the neotropics, it is difficult to test the hypothesis that such supposedly fern-rich habitats (de la Sota, 1971; Wagner & Gómez, 1983; Lellinger, 1985) are indeed relatively more diverse than La Selva. It seems well established that epiphytes in general are most diverse in mid-

elevation cloud forests (Gentry & Dodson, 1987), where such predominantly epiphytic pteridophyte genera as *Lycopodium*, *Hymenophyllum*, *Blechnum*, *Elaphoglossum*, and *Grammitis* have many species in Costa Rica. Wagner and Gómez (1983) maintain that 70% of the total Costa Rican pteridophyte flora consists of epiphytic species, compared with only 41.9% at La Selva. However, it has also been suggested (Gentry & Dodson, 1987) that this increase in epiphytic species with elevation is countered by a corresponding decrease of terrestrial species. Mainly terrestrial genera such as *Selaginella*, *Danaea*, *Adiantum*, and *Tectaria* are perhaps most diverse in the humid lowlands. *Trichomanes*, though largely epiphytic, has many more terrestrial species in the Costa Rican lowlands than at higher elevations (however, the reverse may be true of other genera, such as *Elaphoglossum*). Tree ferns are often associated with cloud forests; for example, Lee et al. (1987) report that tree-fern diversity in the Monte Verde area is highest in "montane rainforest" (1535–1610 m) and declines at lower elevations. However, the total number of tree-fern species in their entire study area (7) is one less than the La Selva total (including *Metaxya*).

At the country level, it may indeed be true that pteridophytes in general are most diverse at mid-elevations, as is apparently the case in Panama (Lellinger, 1985). Still, it is perhaps of interest in this connection that the estimated percentage of pteridophytes in the La Selva vascular flora (9%) is identical to that in the total Costa Rican flora (9.0%, based on 900 pteridophyte species out of an estimated 10,000 vascular plant species). Dogma also has it that endemism and insularity increase as elevation increases. Thus, we might predict that pteridophyte diversity at a particular mid-elevation site would not necessarily exceed that at La Selva, even given that pteridophytes were more diverse at mid-elevations on the country level. Floristic data from a mid-elevation cloud forest locale such as the Monte Verde reserve in Costa Rica would shed much light on this situation.

Elevation is not, of course, the only factor affecting fern distribution. In a previous section of this paper, the important role of precipitation was alluded to. Other factors are not well understood. For example, Finca El Bejuco, a small biological field station only about 7 km away from La Selva and at approximately the same elevation, harbors numerous pteridophyte species never collected from La Selva (among them *Dicranopteris flexuosa*, *Trichomanes ankersii*, *T. polypodioides*, *T. punctatum*, *T. galeottii*, *Cyathea stolzei*, *Elaphoglossum backhousianum*, *Thelypteris leprieurii*, and *Triplophyllum funestum*; A. R. Smith, in litt.). This is perhaps not very surprising, inasmuch as localized distributions of fern species within the boundaries of La Selva itself have already been discussed. Local climatic or edaphic factors or chance vagaries of dispersal may be responsible for these phenomena.

Biogeographical Affinities of the La Selva Pteridoflora

The following analysis is based on data presented in Grayum and Churchill (1988a, 1988b).

About 83.6% of La Selva pteridophyte species are here considered widespread, that is, having neither their northern nor southern limit of distribution in Costa

Rica. About 7% of these (10 species) are pantropical, occurring also in Asia and/or Africa. Approximately ⅔ of the New World species range into the West Indies, the remainder being strictly continental. Twenty-six (92.9%) of the 28 more narrowly distributed species reach their northern limit in Costa Rica, whereas but two (7.1%) apparently reach their southern limit here (*Pseudocolysis bradeorum* and *Tectaria rufovillosa*).

Not a single La Selva pteridophyte species is known to be endemic to Costa Rica. In contrast, Hammel (1986) reported that about 13% of the angiosperm species in his study "appear to be endemic to Costa Rica." Endemism is in general low in ferns as compared with spermatophytes (Smith, 1972); however, Lellinger (1975) reported 17 endemic species from the Chocó—probably owing to the fact that this region is biogeographically, rather than politically, defined.

Thus, the La Selva pteridoflora comprises mostly very wide-ranging species, yet clearly shows evidence of southern rather than northern affinities. Southern affinities were also evident in the six angiosperm families analyzed by Hammel (1986), who commented that such a relationship "should come as no surprise." This is certainly the case with pteridophytes, especially considering the previously discussed connections between the pteridofloras of Central America and the Chocó region.

Endemism is very low or nonexistent among La Selva pteridophytes, which again probably relates to air-dispersal of fern diaspores.

Phenology

Phenological studies on ferns in general are rare (Wagner & Gómez, 1983), and on La Selva ferns rarer still. Despite their abundance and diversity at La Selva, pteridophytes have been the subject of exceedingly few ecological or demographic studies. Herbarium data suggest that *Selaginella eurynota* is seasonally reproductive, producing strobili mainly from November to January. Ongoing studies by J. Sharpe (pers. comm.) have shown that all five La Selva *Danaea* species exhibit pronounced seasonality in the maturation of their fertile fronds. On the other hand, Moran (1986) suggested that *Olfersia* (*Polybotrya*) *cervina* may be continuously reproductive at La Selva. The La Selva Biological Station is obviously an excellent place for studies of this sort, which would help fill a significant void in our understanding of pteridophyte reproductive biology.

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APPENDIX 1. CHECKLIST OF THE PTERIDOPHYTES OF LA SELVA

Species	Habit	Habitat	Abundance	Distr.
	Division Lycopodiophyta			
	Family Selaginellaceae			
Selaginella anceps C. Presl	TEl	A	3	
Selaginella arthritica Alston	Tl	SAd	4	BCI
Selaginella atirrensis Hieron.	Tl	R	4	
Selaginella bombycina Spring	Ee	Q	2	
Selaginella eurynota A. Braun	TLl	AdW	4	
Selaginella flagellata Spring	TLEUl	Ad	4	BCI
Selaginella oaxacana Spring	Tl	AZ	3	
Selaginella silvestris Aspl.	Tl	Ad	1	RP
Selaginella umbrosa Lemaire ex Hieron.	ELTl	RQ	4	
	Family Lycopodiaceae			
Lycopodium cernuum L.	Tl	Rd	1	BCI
Lycopodium dichaeoides Maxon	Ce	P	1	
Lycopodium dichotomum Jacq.	Ce	PA	2	BCI
Lycopodium linifolium L.	CUe	ASPw	3	RP
	Division Polypodiophyta			
	Family Ophioglossaceae			
Ophioglossum reticulatum L.	Te	W	1	BCI
	Family Marattiaceae			
Danaea cuspidata Liebm.	Te	P	1	
Danaea elliptica J. E. Smith	Te	Pr	2	
Danaea grandifolia L. Underw.	Te	PwrZ	1	
Danaea nodosa (L.) J. E. Smith	Te	Pw	3	BCI
Danaea wendlandii Reichb. f.	Te	P	4	
	Gleicheniaceae			
Dicranopteris pectinata (Willd.) L. Underw.	Tl	R	(1)	BCI, RP
Gleichenia bifida (Willd.) Spring	Tl	Rd	2	
	Hymenophyllaceae			
Hymenophyllum brevifrons Kunze	Cl	P	1	BCI
Hymenophyllum hirsutum (L.) Sw.	ULl	P	2	
Hymenophyllum maxonii Christ ex Morton	Ul	P	3	
Hymenophyllum polyanthos (Sw.) Sw.	UCLl	P	3	
Trichomanes angustifrons (Fée) W. Boer	Ul	PA	2	
Trichomanes ankersii Parker ex Hook. & Grev.	Ul	Pr	(1)	
Trichomanes collariatum Bosch	Hl	P	4	RP
Trichomanes crispum L.	Ce	P	1	

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Trichomanes curtii Rosenstock	Ul	P	1	
Trichomanes diaphanum H.B.K.	UEl	QPw	3	
Trichomanes diversifrons (Bory) Mett.	Te	PrA	2	BCI
Trichomanes ekmanii W. Boer	Ul	P	2	BCI
Trichomanes elegans Rich.	Te	Pw	2	
Trichomanes godmanii Hook.	Ul	P	4	BCI
Trichomanes krausii Hook. & Grev.	UEl	QS	3	BCI, RP
Trichomanes membranaceum L.	UEl	Pw	3	RP
Trichomanes osmundoides DC.	Te	R	(1)	
Trichomanes pinnatum Hedwig	Te	Pr	1	BCI
Trichomanes rigidum Sw.	Te	P	1	
Trichomanes tuerckheimii Christ	Ul	Pr	1	
	Metaxyaceae			
Metaxya rostrata (H.B.K.) C. Presl	Ts	Pr	1	BCI
	Cyatheaceae			
Alsophila cuspidata (Kunze) Conant	Ta	SP	4	BCI, RP
Alsophila firma (Baker) Conant	Ta	S	4	
Cyathea microdonta (Desv.) Domin	Ta	RdS	2	BCI
Cyathea multiflora J. E. Smith	Ta	Pw	4	
Cyathea schiedeana (C. Presl) Domin	Ta	Z	1	
Cyathea trichiata (Maxon) Domin	Ta	R	3	BCI, RP
Cyathea ursina (Maxon) Lellinger	Te	Z	2	
	Polypodiaceae			
Adiantum latifolium Lam.	Tl	WRdPw	4	RP
Adiantum macrophyllum Sw.	Ts	R	2	RP
Adiantum obliquum Willd.	Tsl	Pd	4	BCI
Adiantum petiolatum Desv.	Tls	WRd	4	BCI, RP
Adiantum seemannii Hook.	Ts	R	1	BCI
Adiantum tetraphyllum H. & B. ex Willd.	Tsl	ZA	3	BCI, RP
Adiantum wilsonii Hook.	Tl	R	1	
Anetium citrifolium (L.) Splitg.	Ul	PZ	3	BCI, RP
Antrophyum cajenense (Desv.) Spreng.	Us	P	2	
Antrophyum lanceolatum (L.) Kaulf.	Us	SP	3	
Antrophyum lineatum (Sw.) Kaulf.	Us	P	*	
Asplenium abscissum Willd.	Ee	Q	1	
Asplenium cirrhatum Rich. ex Willd.	LEe	P	3	
Asplenium cuspidatum Lam.	CUe	PSA	4	BCI
Asplenium falcinellum Maxon	UCe	P	3	BCI
Asplenium formosum Willd.	LEe	R	2	
Asplenium holophlebium Baker	Ul	Pw	2	
Asplenium otites Link	Ee	Q	2	
Asplenium pteropus Kaulf.	Ue	Pw	1	BCI, RP
Asplenium repandulum Kunze	Es	Q	3	
Asplenium serra Langsd. & Fisch.	UCs	P	3	
Asplenium serratum L.	UCe	P	3	BCI, RP
Blechnum fraxineum Willd.	Te	R	1	
Blechnum occidentale L.	Te	Rd	3	
Blechnum polypodioides Raddi	Te	Pd	1	

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Bolbitis aliena (Sw.) Alston	TEs	QPw	1	
Bolbitis nicotianifolia (Sw.) Alston	Es	Q	3	BCI, RP
Bolbitis nicotianifolia (Sw.) Alston	Hl	PwZ	2	
Bolbitis portoricensis (Sprengel) Hennipman	TEs	QSA	3	BCI
Ctenitis sloanei (Poeppig ex Sprengel) Morton	TLe	RAd	1	BCI
Ctenitis subincisa (Willd.) Ching	Te	SAw	2	RP
Cyclopeltis semicordata (Sw.) J. Smith	Te	S	4	BCI, RP
Dennstaedtia bipinnata (Cav.) Maxon	Tl	AdS	3	
Dennstaedtia cicutaria (Sw.) T. Moore	Tl	R	2	BCI, RP
Dennstaedtia obtusifolia (Willd.) T. Moore	Ts	Pw	2	RP
Dicranoglossum panamense (C. Chr.) L. D. Gómez	Ue	SA	3	BCI
Didymochlaena truncatula (Sw.) J. Smith	Te	Aw	3	RP
Diplazium cristatum (Desr.) Alston	Te	Aw	1	RP
Diplazium grandifolium (Sw.) Sw.	Te	R	1	BCI
Diplazium ingens Christ	Te	Z	1	
Diplazium lindbergii (Mett.) Christ	Te	Z	3	
Diplazium lonchophyllum Kunze	Te	R	2	
Diplazium macrophyllum Desv.	Te	ZPw	3	
Diplazium pactile Lellinger	Te	Z	2	
Diplazium striatastrum Lellinger	Ta	SAZ	4	RP
Elaphoglossum amygdalifolium (Mett.) Christ	Ul	Aw	2	RP
Elaphoglossum herminieri (Bory ex Fée) T. Moore	Cs	P	3	BCI, RP
Elaphoglossum latifolium (Sw.) J. Smith	Cs	P	3	
Elaphoglossum palmense Christ	CUs	P	4	
Elaphoglossum peltatum (Sw.) Urban	Cl	P	3	
Elaphoglossum sp. nov., ined.	Us	Pw	3	
Grammitis linearifolia (Desv.) Steudel	Ce	PA	4	
Grammitis serrulata (Sw.) Sw.	CLl	PA	3	
Grammitis turrialbae (Christ) Seymour	Us	P	*	
Hecistopteris pumila (Sprengel) J. Smith	CLl	P	2	
Hemidictyum marginatum (L.) C. Presl	Te	R	1	BCI, RP
Hemionitis palmata L.	TLe	WAd	4	
Hypolepis hostilis (Kunze) C. Presl	Tl	Pd	4	
Hypolepis repens C. Presl	Tl	WAd	4	
Lastreopsis exculta (Mett.) Tindale subsp. *guatemalensis* (Baker) Tindale	Ts	R	3	
Lindsaea lancea (L.) Bedd. var. *lancea*	Ts	Pr	1	
Lindsaea quadrangularis Raddi subsp. *subalata* Kramer	Ls	Prw	1	
Lomariopsis fendleri D. Eaton	Hl	P	4	BCI
Lomariopsis japurensis (Martius) J. Smith	Hl	SAd	3	RP
Lonchitis hirsuta L.	Tes	RAwSw	3	
Nephrolepis biserrata (Sw.) Schott	TULe	SWZMPd	4	BCI
Nephrolepis multiflora (Roxb.) Jarrett ex Morton	TUe	S	2	
Nephrolepis pendula (Raddi) J. Smith	Ue	A	3	BCI, RP
Nephrolepis rivularis (Vahl) Mett. ex Krug	UCe	P	2	
Oleandra articulata (Sw.) C. Presl	ULCl	P	2	
Pityrogramma calomelanos (L.) Link	Te	WRd	3	BCI, RP
Pityrogramma tartarea (Cav.) Maxon	Te	Rd	(1)	

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Polybotrya alfredii Brade	HUl	P	1	
Polybotrya caudata Kunze	Hl	P	4	BCI
Polybotrya cervina (L.) Kaulf.	LTs	Pd	4	
Polybotrya osmundacea H. & B. ex Willd.	HTl	ZP	3	RP
Polypodium angustifolium Sw.	Cs	Z	2	RP
Polypodium aureum L.	UCs	SP	3	
Polypodium ciliatum Willd.	CUl	SA	4	BCI, RP
Polypodium crassifolium L.	Us	RZQ	2	BCI
Polypodium dissimile L.	Us	SAQ	3	
Polypodium furfuraceum Schlecht. & Cham.	Cs	PA	3	
Polypodium hygrometricum Splitg.	UEl	SR	2	BCI
Polypodium loriciforme Rosenstock	UCl	PS	4	
Polypodium lycopodioides L.	Cl	SPA	4	BCI
Polypodium maritimum Hieron.	Cl	AP	3	BCI, RP
Polypodium occultum Christ	Us	ZA	2	BCI
Polypodium pectinatum L.	UCs	AS	3	BCI
Polypodium percussum Cav.	CUl	AP	4	BCI, RP
Polypodium phyllitidis L.	Us	SA	4	
Polypodium sororium H. & B. ex Willd.	Ul	P	3	
Polypodium sphenodes Kunze ex Klotzsch	Ul	ZQP	2	
Polypodium triseriale Sw.	Cl	P	3	BCI
Pseudocolysis bradeorum (Rosenstock) L. D. Gómez	Ul	QSZR	2	
Pteris altissima Poiret	Tes	ZAws	3	BCI, RP
Pteris propinqua Agardh	Te	AdW	2	BCI
Pteris pungens Willd.	Te	P	3	BCI
Pteris quadriaurita Retz.	Te	Rd	(1)	
Saccoloma inaequale (Kunze) Mett.	Te	Pd	4	
Salpichlaena volubilis (Kaulf.) J. Smith	Tv	P	4	
Stigmatopteris longicaudata (Liebm.) C. Chr.	Te	Q	1	
Stigmatopteris nephrodioides (Klotzsch) C. Chr.	Te	Z	1	
Tectaria athyrioides (Baker) C. Chr.	Tes	Z	3	
Tectaria brauniana (Karsten) C. Chr.	Ts	Pw	2	
Tectaria draconoptera (D. Eaton) Copel.	Te	Pw	3	
Tectaria incisa Cav.	TEe	SAwQR	4	BCI, RP
Tectaria mexicana (Fée) Morton	TEs	RAd	4	
Tectaria nicotianifolia (Baker) C. Chr.	Tl	AS	3	BCI, RP
Tectaria plantaginea (Jacq.) Maxon	Es	Q	2	
Tectaria rivalis (Mett. ex Kuhn) C. Chr.	Te	A	2	
Tectaria rufovillosa (Rosenstock) C. Chr.	Te	P	1	
Thelypteris angustifolia (Willd.) Proctor	TLs	R	2	RP
Thelypteris balbisii (Sprengel) Ching	TLe	R	4	BCI
Thelypteris biolleyi (Christ) Proctor	Te	S	2	
Thelypteris curta (Christ) Reed	Te	A	3	
Thelypteris decussata (L.) Proctor	Te	Pdw	2	
Thelypteris dentata (Forssk.) E. St. John	TLs	WQ	4	BCI, RP
Thelypteris falcata (Liebm.) R. Tryon	TLs	PwS	2	
Thelypteris francoana (Fourn.) Morton	TLe	R	3	RP
Thelypteris ghiesbreghtii (Hook.) Morton	Tl	S	3	
Thelypteris gigantea (Mett.) Morton	TLEs	QZ	1	RP

APPENDIX 1. CONTINUED

Species	Habit	Habitat	Abundance	Distr.
Thelypteris hispidula (Decne.) Reed	Te	S	2	
Thelypteris leprieurii (Hook.) R. Tryon	TEe	R	(1)	
Thelypteris lingulata (C. Chr.) Morton	Ts	P	4	
Thelypteris nicaraguensis (Fourn.) Morton	TLEe	SQW	4	BCI
Thelypteris poiteana (Bory) Proctor	Tl	W	2	BCI, RP
Thelypteris resinifera (Desv.) Proctor	Te	R	1	RP
Thelypteris serrata (Cav.) Alston	TLs	RMQ	2	BCI
Thelypteris torresiana (Gaud.) Alston	Ts	RAd	4	BCI, RP
Thelypteris urbanii (Sodiro) A. R. Smith	Te	Aw	2	
Thelypteris villana L. D. Gómez	ETe	Q	(1)	
Vittaria costata Kunze	Us	SP	2	BCI
Vittaria lineata (L.) J. E. Smith	CUEe	AP	3	BCI
Vittaria stipitata Kunze	CUe	PA	3	

LEGEND FOR APPENDIX 1

Habit.—Two types of information are encoded here: the substrate is indicated by a capital letter, and the nature of the rhizome by a lower-case letter.

C—Canopy epiphytes; sometimes found closer to the ground, as in light gaps or pejibaye trunks; may be frequently encountered on branchfalls.

E—Epipetric; growing on rocks or, occasionally, concrete.

H—Hemiepiphytes; species which begin life on the ground, or very close to it, and at maturity are characteristically appressed-climbers on trunk bases (the connection with the ground commonly being lost).

L—Log-dwellers; species that are typically found growing on rotting logs or, occasionally, timber (epiphytes may persist on fallen trees for some time, and many terrestrial species are occasionally seen on logs as well).

T—Terrestrial species.

U—Understory epiphytes; including mainly trunk epiphytes, having no close association with the ground.

a—arborescent; species with a distinct, self-supporting trunk of at least 0.5 m in height.

e—erect; species with a short, erect rhizome, the fronds closely approximate in a rosette (most terrestrial ferns fit this description).

l—long-creeping rhizome, the fronds arising rather distantly.

s—short-creeping rhizome, the fronds more or less approximate and often clustered at the apex.

v—vining; ferns with an erect rhizome, climbing high into adjacent foliage by means of the greatly elongated frond axes (at La Selva, only a single species falls into this category).

For either of the two subcategories of "Habit" (as well as for the "Habitat" subcategories) two or more alternative conditions may be indicated for a given species. These are always listed in order of prevalence: thus, "CUe" describes a species with erect rhizome which is predominantly a canopy epiphyte, but sometimes occurs in the understory; similarly, "Tls" would be used to characterize a terrestrial species with rhizomes that are long-creeping, or sometimes short-creeping.

Habitat.—This category regularly has one component, and sometimes a second. The broad habitat preference is always indicated by a capital letter. A microhabitat within that habitat may be specified by the use of an appropriate lower-case letter.

A—Alluvial forest; forest which exists on alluvial soils, especially along the major rivers and in the vicinity of the Quebrada (Q.) Leonel, and near the lower reaches of the Q. El Salto, Q. El Surá (including the Arboretum) and Q. Sábalo.

M—Marshes; open, treeless, wet sites (a very poor fern habitat at La Selva).
P—Primary forest; comparatively well-drained slopes and plateaus in upland primary forest, the habitat that prevails over most of La Selva.
Q—Quebradas; small, usually rocky, fast-moving streams, and similar sections of larger streams (e.g., the Q. Esquina, and the Q. El Salto beyond line 2800).
R—Riparian; the banks of the larger rivers, as well as the lower portions of the Q. El Salto, Q. Sábalo and Q. El Surá.
S—Secondary forest; includes abandoned cacao plantations and formerly cleared land in various stages of regeneration. Since much of this habitat at old La Selva occurs in areas of former alluvial forest, the two subcategories are not always clearly defined.
W—Weedy land; regularly maintained or recently abandoned clearings, groves, pastures, etc. The pejibaye grove, the station clearing and first-year successional strips are good examples.
Z—Swamp forest; forested swampy areas, as exemplified by most of Plot II; many of the species of this habitat also occur along sluggish sections of streams.
d—disturbed areas, such as light gaps, landslides or trailsides.
r—ridges or hilltops, generally toward the back of the property.
w—wet or damp, low-lying sites, often near streams or marshes, or on seeps.

Abundance.—The estimates of abundance are relevant only within the context of the habitat of the fern under consideration.

1—very rare; known from only 1–2 collections. The casual observer should not expect to encounter any of these.
2—rare; known from 3–5 collections. The casual observer might expect to encounter some of the species in this category, but no given one.
3—occasional; widely scattered but nowhere common, or else locally abundant. The casual observer has a good chance of seeing any of these.
4—abundant; the casual observer, in the right habitat, will be hard-pressed to overlook these species.
( )—hypothetical; species not known from La Selva proper, but collected in immediately adjacent areas–usually the "Cloud Forest Ridge," or along the Río Peje.
* —dubious; species indicated for La Selva by properly identified collections believed to incorporate label errors as to locality.

Distribution.

BCI—species shared with Barro Colorado Island, Panama.
RP —species shared with the Río Palenque Science Center, Ecuador.